Short-term pain for long-term gain: A hypothetical role for the mantle in coleoid cephalopod circulation*

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Abstract: Mantle cavity pressures are frequently hypothesized to drive venous return in the high-output circulatory systems of coleoid cephalopods. However, studies using non-invasive, imaging ultrasound on resting cuttlefish (*Sepia officinalis* Linnaeus, 1758) conclude that mantle cavity pressures do not drive venous return. Interestingly, data from cuttlefish showing sustained mantle hyperinflation indicate instead that forces within the mantle's tissues could aid circulation. We hypothesize that alternating contractions of the radial and circular mantle muscles create a bellows-like effect on mantle capillaries. This effect could be propulsive during normal ventilation and jetting but could stop circulation when the cuttlefish is engaged in sustained mantle hyperinflation. Sustained mantle hyperinflation accompanies some behaviors, for example the Deimatic Display. The metabolic consequences of strangulated circulation might limit the duration of these behaviors.

Key words: cardiovascular dynamics, peripheral circulation, mantle cavity pressure, *Sepia officinalis*, veins

The circulatory system of coleoid cephalopods is closed and has two separate loops: one though the gills, powered by the two branchial hearts, and one through the body, powered by the single systemic heart (Tompsett 1939). During exercise, increases in systemic heart rate and stroke volume, combined with increasing arterial pressure (Wells and Smith 1987), result in the work and power output of systemic heart tissue rivaling or exceeding those of mammals (Shadwick *et al.* 1990, O'Dor and Webber 1991). The coleoid hearts are generally considered insufficient to generate such power output and many authors ascribe an accessory circulatory function to the contractions of the coleoid mantle. The mantle encloses most organs (including the hearts, large veins, and large arteries) in a space called the mantle cavity (Tompsett 1939). At rest, the mantle expands and contracts to move water through the mantle cavity and over the gills. Maximum mantle cavity pressures in resting cuttlefish are around 0.16 kPa (King, pers. obs.). During jetting, the muscular mantle contracts forcefully, increasing maximum mantle cavity pressures by over an order of magnitude to at least 5.5 kPa in cuttlefish (O'Dor and Webber 1991), 8 kPa in octopods (Wells *et al.* 1987), and 6.6 kPa in squid (O'Dor and Webber 1991). Could the forces generated by the muscular mantle help circulate the large amounts of blood needed during exercise?

One model suggests that the hearts should contract at the same time as the mantle. The resulting increase in mantle cavity pressure could augment arterial pressure generated by the heart, driving blood to the low-pressure periphery outside the mantle cavity. Additionally, the slightly negative mantle cavity pressures created during mantle expansion could help to pull venous blood back into the mantle cavity from the head and arms and toward the hearts. However, a 1:1 ratio of heart to mantle contractions is not usually observed in octopods (Wells 1978, Smith 1982), squid (Shadwick *et al.* 1990), or cuttlefish (Chichery 1980, King *et al.* 2005, King and Adamo 2006), even during jetting. Moreover, the ratio of contractions between the heart and the mantle can change over time within the same octopus (Johansen and Martin 1962, Wells 1978) or cuttlefish (King *et al.* 2005). It would seem that heart contractions are not tied to mantle contractions in any fixed way.

In a different model, mantle cavity pressures could drive blood flow in the veins, instead of by helping the heart. Pressures have been measured in the vena cava cephalica (probably the lateral vena cava of King *et al.* 2005) and efferent gill vessel of the octopus *Enteroctopus dofleini* (Wülker, 1910) (Johansen and Martin 1962) and the squid *Loligo pealeii* (Lesueur, 1821) (Bourne 1982). In these vessels, there are two overlaid pressure pulses: one that is rela-

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tively slow and large and one that is relatively fast and small (Fig. 1A). The slow, large pulse (Fig. 1B) is due to ventilatory movements (Johansen and Martin 1962). The fast, small pulse (Fig. 1C) is due to venous contraction (King *et al.* 2005). Probably due to the large size of the ventilatory pulse, many have suggested that the mantle cavity pressure flattens large, thin-walled veins such as the venae cavae and the efferent branchial vessels. However, for the veins to flatten, the compression-resistant blood inside them would have to move into the adjacent vasculature. To accomplish this, mantle contractions would have to generate pressure differences between the anterior and lateral venae cavae or between the efferent branchial vessel and the systemic heart. Theoretically, the pressures created in the mantle cavity, while large at times, are applied equally to all veins within the cavity, and therefore would not create the pressure dif-

ferences required to move blood between vessels. So, while the contractions of the mantle create absolute pressure changes in the vessels, they are unlikely to be propulsive because they are unlikely to change the relative pressure between the vessels.

Empirical data do not support the hypothesis that mantle cavity pressure compresses the veins. If mantle cavity pressures did compress the veins, we would have two expectations: (1) the veins would contract at the same rate as the mantle and (2) the veins would collapse as a unit along their length as mantle pressure increased. Neither of these occurs in experimental observations using imaging ultrasound. First, the lateral venae cavae and efferent branchial vessels do not contract at the same rate as the mantle and, therefore, could not be compressed by it (King *et al.* 2005). Second, the only large vein that does contract at the same rate as the mantle in resting cuttlefish, namely the anterior vena cava, contracts peristaltically and not as a unit along its length (King *et al.* 2005). Furthermore, this vein's contractions become unsynchronized with mantle contractions in a mating female; the vein's contractions remain steady and slow during the rapid and vigorous mantle contractions that accompany the placement of the male's arm in her mantle (King 2005). The anterior vena cava is evidently able to contract independently of the pressures generated in the mantle cavity. It would seem that pressures in the mantle cavity do not compress the large veins.

Not only are contractions of mantle not propulsive in the veins but also they could impede venous blood flow from the head and arm veins into the anterior vena cava. Increased mantle cavity pressure would increase the pressure in the anterior vena cava without increasing pressure in the venous spaces of the head and arms, thus inhibiting the forward flow of blood (Wells *et al.* 1987).

We have found no experimental evidence that supports a role for increasing mantle cavity pressure in venous return. However, some experimental evidence suggests that mantle tissue may play a role in circulation. In this paper, we synthesize this evidence and present a new hypothetical role for


Figure 1. A, Pressure trace from the efferent branchial vessel measured *in vivo* by Johansen and Martin (1962). It consists of two superimposed pressure pulses of different frequencies: a slow and large pulse caused by ventilatory movements (B) and a faster and smaller pulse caused by venous contractions (C). The base pressure of 1.5 kPa is arbitrarily assigned to the pressure trace in C.

the mantle in circulation. We also present additional indirect experimental evidence that supports our hypothesis.

HYPOTHETICAL ROLE FOR MANTLE TISSUE

The mantle may aid circulation by creating pressure within its own tissues, instead of by creating pressure in the mantle cavity. This hypothesis was spurred by experimental results from cuttlefish (*Sepia officinalis* Linnaeus, 1758). When cuttlefish are exposed to a sudden visual stimulus, heart rates drop and mantles hyperinflate for several seconds (King and Adamo 2006). Mantle hyperinflation is an expansion greater than during normal ventilation (King and Adamo 2006). Interestingly, a decrease in heart rate occurred almost simultaneously and proportionally to the mantle's hyperinflation (King and Adamo 2006). This coincidence initiated our interest in the connection between mantle tissue and circulation. To explain the connection we draw, we first present a summary of mantle tissue structure.

Cuttlefish mantle tissue is composed almost exclusively of two muscle types, radial and circular muscles (Fig. 2, Bone *et al.* 1994). Radial muscles contract to expand the mantle cavity during ventilation (Bone *et al.* 1994). Circular muscle contraction constricts the mantle cavity only during heavy ventilation and jetting (Bone *et al.* 1994). Both sets of muscles are partially antagonized by variously arranged col-
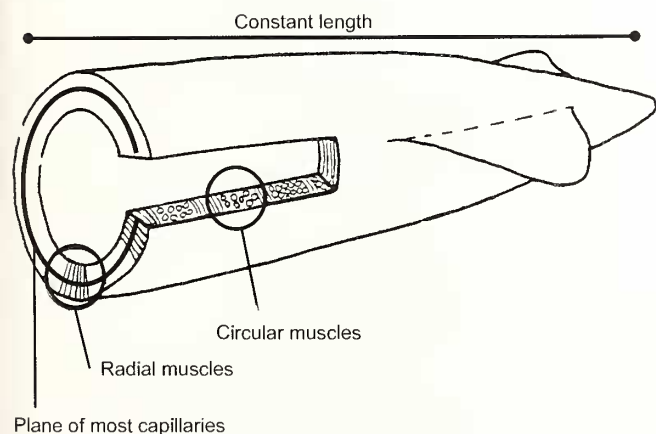

Figure 2. The bands of radial and circular muscles in the decapod mantle and the plane along which most capillaries are aligned. Radial muscles contract to thin mantle tissue and expand the mantle cavity. Circular muscles contract to thicken mantle tissue and constrict the mantle cavity. Collagen tunics ensure that the mantle does not change length during mantle contraction and expansion. Most capillaries are perpendicular to the radial muscles and parallel to the circular muscles. After Shadwick (1994).

lagen tunics and by each other during all but resting ventilation (Bone *et al.* 1994). The collagen tunics keep the decapod mantle the same length so that contractions of the different muscles translate only into expansion and constriction of the mantle.

Most capillaries in the mantle are oriented perpendicularly to the radial muscles (Fig. 2, Bone *et al.* 1981). We suggest that they could be compressed by radial muscle contraction (Fig. 3A). Conversely, the capillaries are oriented parallel to the circular muscles (Bone *et al.* 1981), and therefore, we suggest, would not be compressed by circular muscle contraction, and in fact could be expanded by it (Fig. 3C). The radial muscles are always used to expand the mantle, albeit minimally, during resting ventilation (Bone *et al.* 1994). In our model, the radial muscles always alternate between creating a gentle force pushing blood out of the capillaries (radial muscle contraction, Fig. 3A) and creating a vacuum in the capillaries that draws blood in (radial muscle relaxation, Fig. 3B). Mantle expansion could thus drive the flow of blood from the mantle into the veins, while mantle constriction could aid the flow of blood from the arteries into the mantle. Even during rest, this would help power peripheral circulation. We hypothesize that this effect would be magnified during jetting when radial muscles contract more vigorously, expelling more blood, and when the circular muscles become active, possibly contributing to capillary dilation (Fig. 3C). The alternating contractions of the radial and circular muscles could create greater peripheral pumping forces to help power circulation during exercise.

More experiments are needed to test this hypothesis. For example, it is unclear whether changes in capillary length would offset changes in their diameter. Certainly, if capillaries were completely occluded by radial muscle contraction, no change in length would compensate. For anything other than complete occlusion, the situation is less clear. Unfortunately, almost no direct observations have been made on blood flow in the periphery which, considering the strength and size of the mantle, hinders our understanding of integrated cardiovascular dynamics (Bourne 1984). Nevertheless, several indirect lines of data support our hypothesis that mantle muscle contraction influences peripheral circulation.

After exposure to a sudden visual stimulus, cuttlefish and octopods hyperinflate their mantles for several seconds, and their hearts slow or stop beating (King and Adamo 2006). Mantle hyperinflation is achieved by forceful contraction of the radial muscles (Bone *et al.* 1994). If our hypothesis were correct, we would expect mantle hyperinflation to dramatically increase peripheral resistance, causing aortic pressure to remain elevated despite slowing or stopping of the heart. Elevated aortic pressure is in fact maintained in
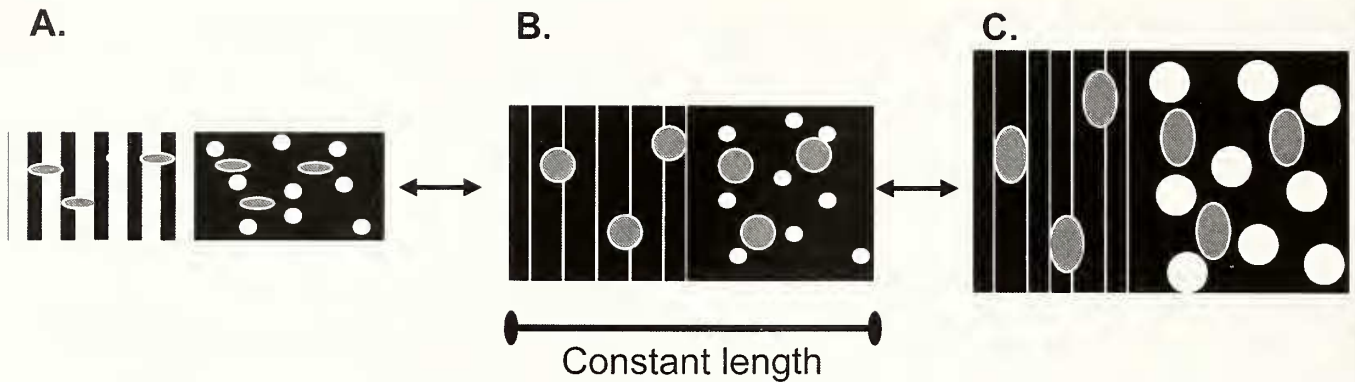
Figure 3. A hypothetical cross-section of mantle tissue during radial muscle contraction (A), relaxation of both muscle sets (B), and circular muscle contraction (C). This cross-section is along the same plane that shows the circular muscles in Fig. 2. The mantle cavity is above the blocks, the open water below. The vertical white lines represent the radial muscles and the white circles represent the circular muscles. Active muscles are represented by heavier lines and circles. The shaded circles represent the capillaries. Capillaries are hypothetically occluded during radial muscle contraction (A) and hypothetically expanded during circular muscle contraction (C). This could propel blood during normal ventilation and jetting.

Enteroctopus dofleini during mantle hyperinflation and cardiac arrest (Johansen and Martin 1962). Furthermore, if our hypothesis were true, we would expect that the veins would fill during cardiac slowing and stopping and mantle hyperinflation, the blood originating from the compressed capillaries in the mantle. The veins and systemic heart in fact do fill at this time (King 2005).

Further evidence is available from jetting cephalopods. Brief mantle hyperinflation starts every jetting cycle. The heartbeat of octopods is interrupted during jetting, although it was not noted whether this is during mantle hyperinflation or water expulsion (Johansen and Martin 1962, Wells *et al.* 1987). During hyperinflation, the radial muscles might compress the mantle capillaries, greatly reducing blood flow through the mantle. The cuttlefish or octopus heart slows or stops at this time, perhaps to avoid dangerous pressure increases in the head and viscera, where blood can still flow. By contrast, when *Octopus vulgaris* Cuvier, 1797 moves using its arms, cardiac interruption is not seen and in fact heart rate increases (Wells *et al.* 1987). It seems that movement does not affect cardiac function unless the movement is achieved using mantle hyperinflation. Interestingly, the mean resistance of the peripheral vessels remains constant or even decreases during mantle contractions (exercise) in octopods (Wells *et al.* 1987) and squid (Shadwick *et al.* 1990). The contractions of the circular muscles during exercise might dilate mantle capillaries, resulting in periods of lowered resistance between the periods of increased resistance associated with radial muscle contraction. The alternating high and low resistance could result in no change or a drop in the mean resistance. Our hypothesis is, thus, consistent with most existing indirect evidence in the literature.

CONCLUSIONS

Currently, we do not have enough data to understand the effects of mantle contraction on the circulation of coleoid cephalopods. The complete picture should integrate the effects of fluctuating pressures in the arteries and veins relative to the periphery during mantle contractions, the effects of the contractions of circular and radial mantle muscles on mantle capillaries, and the effects of the contracting veins. Differences in lifestyle and anatomy may mean this integrated picture differs from one group of coleoid cephalopods to the next. Also to be integrated into the complete circulatory picture are the effects of the accessory vasoconstricting organs found in both cuttlefish and squid on the inside surface of the mantle, around the posterior pallial arteries and veins (Alexandrowicz 1962). Their structure has been well described, but their function is not clear, including whether they contract during contractions of the circular (mantle constriction) or of the radial (mantle expansion) mantle muscles, why they appear on the posterior but not the anterior pallial vessels, and why they do not appear in octopods at all. What is clear is that further research is needed on these accessory vasoconstricting organs and the other factors affecting peripheral circulation.

With new technology being adopted from medicine, the area of integrated cephalopod cardiovascular dynamics promises to be interesting and rewarding in the future. To spur further research, we present a hypothesis for verification—that the mantle could contribute to circulation during ventilation and jetting by alternately compressing and expanding the capillaries in its own tissues. However, strong, maintained contractions of the radial muscles (sustained hy-

perinflation) may strangulate blood flow (King and Adamo 2006). What might be useful during normal ventilation and locomotion might, thus, be non-adaptive in some acute cases such as the sustained hyperinflation exhibited after a sudden stimulus. This hypothesis is supported by indirect evidence from the literature but requires further investigation. If our hypothesis were supported by direct evidence, it would have consequences for the behaviors that involve sustained mantle hyperinflation, such as the Deimatic Display. The duration of such behaviors may be limited by how long a given animal can forgo normal circulation.

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